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Will the Expansion of Northern Snakehead Negatively Affect the Fishery for Largemouth Bass in the Potomac River (Chesapeake Bay)?

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MANAGEMENT BRIEF

Will the Expansion of Northern Snakehead Negatively Affect the Fishery for Largemouth Bass in the Potomac River (Chesapeake Bay)?

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Abstract
A modeling study was conducted to determine if the expansion of invasive northern snakehead *Channa argus* could negatively affect the largemouth bass *Micropterus salmoides* population size in Potomac River (Chesapeake Bay). Current distributions for both species were generated using catch records. Northern snakehead was not widely distributed during the study period and occurred mainly in upstream areas of tributaries. Many of these areas were moderately or highly suitable habitats for largemouth bass. Of sites where juvenile largemouth bass were collected, 10.6% were associated with northern snakehead. Using population modeling and measured predator–prey interactions, we determined that this level of co-occurrence would result in a 3.8% reduction in largemouth bass population size. This prediction is consistent with current observations that indicate there has not been a negative trend in the largemouth bass fishery. As co-occurrence was increased in the model, however, the negative impact of northern snakehead on largemouth bass monotonically increased. The time required for such increases in northern snakehead distribution is not known. If northern snakehead continues to expand its range in the absence of control measures, then our population model, with its assumptions, predicts a 35.5% reduction in the abundance of largemouth bass in the Potomac River.

Northern snakehead *Channa argus* is native to Asia, but has been recently collected in Maryland and several other states in the USA (Fuller et al. 2012). It was first reported in the Potomac River, Virginia, in 2004 (Orrell and Weigt 2005) and has rapidly expanded its distribution throughout the drainage and into Maryland (Odenkirk and Owens 2007). The species has a high risk of invasiveness (FISK Score = 28, Copp et al. 2009; J. J. Newhard, unpublished data). It is possible that northern snakehead will cause declines in biomass of some native fish species (Courtenay and Williams 2004; Jiao et al. 2009), but its impact on naïve ecosystems has not been well-documented. Other invasive fishes such as white perch *Morone americana* and black carp *Mylopharyngodon piceus* have caused problems for ecosystems (Johnson et al. 1990; Chick and Pegg 2001; Herborg et al. 2007). Northern snakehead and largemouth bass *Micropterus salmoides*, another top predator, share similar habitats (Lapointe et al. 2010) and significant levels of prey resources (Saylor et al. 2012). Juveniles for both species are probably competitors as well, though food habits for age-0 northern snakehead are not well-known. In addition, adults of both species consume the other's offspring (J.J.N., unpublished data). It is not known how predation of adult northern snakehead on age-0 largemouth bass will influence either the bass' population or the fishery.

Largemouth bass constitutes a valuable fishery to Maryland's recreational anglers. Originally introduced from the Ohio River basin to Potomac River in the last 1880s as a game fish, largemouth bass is arguably the most valuable recreational sport fish in Maryland. It is sought by many competitive and noncompetitive catch-and-release anglers (USFWS 2008; MDDNR 2012). These anglers have expressed widespread concern in controlling expansion of northern snakehead for the sake of the largemouth bass fishery (J. W. Love, unpublished data). Similar concerns have prompted large-scale northern snakehead eradication projects in Piney Creek, Arkansas, and in Crofton Pond, Maryland. Effects of their introductions on the ecosystem are not known because of insufficient empirical data. However,

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natural history information is available for both species to model their ecological interactions (Landis et al. 2011; Love 2011; MDDNR 2012). We used a population model of largemouth bass to address how expansion of northern snakehead may potentially impact the largemouth bass fishery in the Potomac River.

Objectives of this project were to (1) determine whether adult northern snakehead were distributed in suitable habitats of largemouth bass and the level of co-occurrence, (2) evaluate potential impacts of northern snakehead on largemouth bass, and (3) determine if increased frequency of co-occurrence would negatively affect the largemouth bass population or the fishery. We tested two hypotheses: (1) the co-occurrence of largemouth bass and northern snakehead would negatively affect largemouth bass population size and proportion of larger fish in the population (indicative of problems with the fishery); and (2) the effect of northern snakehead depended on exploitation rates of largemouth bass in the fishery.

METHODS

Collections of largemouth bass (2008–2010) and northern snakehead (2009–2011) were made during autumn (September–November) at sites throughout tidal freshwater areas of the Potomac River. Ninety-six shoreline sites were randomly sampled for 250 linear meters using boat electrofishing as part of Maryland Department of Natural Resource's Tidal Bass Survey (Smith-Root 9.0 GPP; 60 Hz pulse frequency). Sites were randomly selected from all potential shoreline sites using a stratified design; details are given in Love (2011). In addition to data from the Tidal Bass Survey, data from 26 additional sites surveyed by the U.S. Fish and Wildlife Service (USFWS) were used to more completely delineate the distribution of this species. The USFWS identified sites where northern snakehead were likely to occur and sampled them using boat electrofishing. During that sampling, only occurrence of northern snakehead was recorded and, therefore, these data were not used in estimates of co-occurrence (below). Fish were counted and measured (total length [TL] in millimeters). Sites where largemouth bass and northern snakehead occurred were plotted using ArcGIS version 10.0 (ESRI).

Occurrences of juvenile largemouth bass (<200 mm TL) and northern snakehead during the Tidal Bass Survey were used to calculate co-occurrence between species. We used occurrence data rather than density or choropleths in order to simplify calculations of co-occurrence and model runs. Sites where largemouth bass and northern snakehead were collected together were noted as a site of co-occurrence. Their occurrence in the sample was considered relevant for establishing co-occurrence because largemouth bass typically travel small linear distances (e.g., <100 m; Pribyl et al. 2005; J.W.L., unpublished data), and movement of northern snakehead within a season is limited for the majority of individuals (J.J.N., unpublished data). Co-occurrence was analyzed by subwatershed area rather than by stream (i.e., within each Maryland Department of Environment [MDE] 12-digit subwatershed). Individual locations within streams can be biased by sampling intensity such that these locations do not effectively represent the distribution at the drainage basin scale (Fisher and Rahel 2004). Thus, for each subwatershed (see below), the number of sites with co-occurrence was divided by the number of sites with juvenile largemouth bass present to generate a percent occurrence. In addition, this percentage was calculated at the scale of the sampled Potomac River basin.

To determine if northern snakehead frequently occurred in suitable habitat for largemouth bass, a habitat suitability map of largemouth bass was created (Love 2011). Habitat suitability indices (HSIs) were calculated for 23 subwatershed areas of the Potomac River. These areas were delineated by MDE 12-digit codes (MDDNR 1998), which were based on contours for third-order stream drainages (U.S. Geological Survey 7.5-min quadrangle maps; Strahler 1952). For each subwatershed area, appropriate water quality and habitat complexity variables were measured to determine the HSIs. When available in the subwatershed area, water quality was recorded from deployed buoys maintained by the Chesapeake Bay Program and Maryland Department of Natural Resources' (MDDNR) Eyes on the Bay Program (www.chesapeakebay.net) (Figure 1). Water quality variables measured were: average water temperature (°C) during the June–September growing season; average dissolved oxygen (mg/L) during the growing season; average pH during the growing season; maximum monthly salinity (‰) for the year; and water clarity as Secchi disk depth (m) averaged across months. The coverage of submerged aquatic vegetation (SAV) within each subwatershed area was determined from aerial imagery that was geoprocessed by the Virginia Institute of Marine Science (VIMS 2010). Stream discharge data were obtained from the U.S. Geological Survey (waterdata.usgs.gov/nwis/rt). Because stream discharge data were not recorded within the subwatershed area, discharge data used for the subwatershed area were those measured at the closest station measuring discharge into the subwatershed area (Figure 1). In cases when subwatershed areas did not have a water quality buoy, and hence no water quality data available, the average of HSI values calculated for surrounding subwatershed areas was used.

To estimate the level of predation by northern snakehead (500–598 mm TL) on co-occurring, age-0 largemouth bass (<200 mm TL), we used a series of experimental tanks from 3 to 26 August 2011. Indoor experimental tanks were 3.33 m in diameter and 0.67 m water depth with a flow-through system of filtration. Water temperature ranged from 24.4°C to 28.9°C. In each tank, a Styrofoam square (1 × 1 m) was used to float the center of a mesh net (12 mm mesh) that draped over the experimental tank. The size of northern snakehead used in the experiment is similar to the average-sized adult surveyed in the Potomac River in 2009–2011 (mean = 565 mm, SD = 154, n = 1,668). Two randomly selected northern snakehead were starved for 48 h and added to experimental tanks for each experiment.

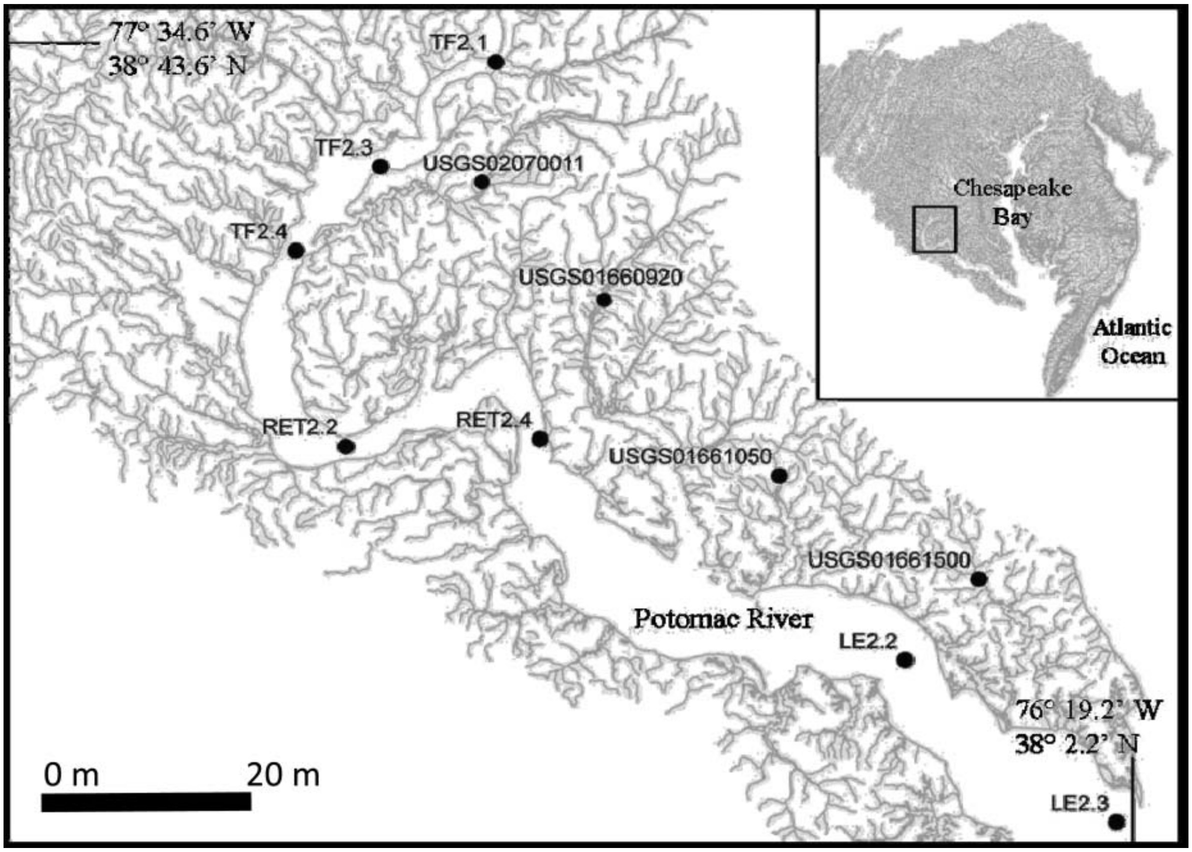

FIGURE 1. Potomac River (Chesapeake Bay) and illustrated distribution of water quality monitoring stations and U.S. Geological Survey stream discharge stations.

Age-0 largemouth bass individuals were acclimated to experimental tank conditions at least 24 h before exposure to predators. The largemouth bass ranged in size from 70 to 170 mm, but were grouped into three size-groups with differing numbers of age-0 bass in each trial (n), depending on their availability: 70–99 mm ($n = 3$, 4, 5, and 5); 100–150 mm ($n = 1$, 2, and 4), and >150 mm ($n = 1$, 1, and 1). Size-groups were used to minimize cannibalism among juveniles (Bettoli et al. 1992). Once added, age-0 largemouth bass individuals were counted daily for 1 week. After each experiment, the proportion of bass surviving was calculated and used in subsequent population models.

Population model.—Potential impacts of northern snakehead on largemouth bass populations were assessed using a population model of relative abundance of each age-class (ages 0–13) for largemouth bass created in Microsoft Excel (version 2003). For each age-class, mean length at age was determined using a von Bertalanffy growth function (VBGF). Parameters and variances used to generate length at age were estimated with data collected for the Potomac River population of largemouth bass from 1999 to 2004 (Cloern and Nichols 1978; Gwinn et al. 2010; MDDNR 2012). Ages were determined using otoliths (Buckmeier and Howells 2003). Parameters obtained from 1999 to 2004 were used because this was the time period prior to expansion of northern snakehead in the Potomac River (Table 1). Relative abundance of largemouth bass in each length-at-age-group depended on natural mortality, the age-groups' vulnerability to fishing gear, fishing mortality, and impact by co-occurring northern snakehead.

Natural mortality (M) of largemouth bass of ages 1+ was estimated using the equation provided in Pauly (1980), incorporating mean water temperature data (16.1°C) and VBGF parameters estimated for the Potomac River population (Table 1). An SD value that was 20% of M was used because the coefficient of variation in M was approximately 0.20 when using additional methods of calculation provided in Hewitt and Hoenig (2005). Natural mortality of age-0 largemouth bass was estimated as 10% annual survivorship with 20% variation in M for age-0 bass. Age-0 bass natural mortality was estimated using data collected from MDDNR Joseph Manning Hatchery, where survivorship from hatching to 75 mm in habitats without refugia was as low as 9% (J.W.L., unpublished data). Because small age-0 individuals were expected to suffer greater levels of overwinter mortality (x) than larger age-0 individuals (Post et al. 1998), the proportion of largemouth bass <100 mm surviving

TABLE 1. Parameter estimates (and SD) used in an age-structured population model of largemouth bass from the Potomac River (Chesapeake Bay watershed, Maryland). Unless noted, a normal distribution of variance was assumed for SD.

Parameter	Symbol	Estimate (SD)
Growth constant	K	0.33 (0.11)
Length infinity	L_∞	424.06 (27.39)
Age at size 0	t_o	0 (0)
Initial length	L_o	144.23 (25.70)
Natural mortality, at age 1+	$M_{\text{age-1+}}$	0.32 (0.06)
Natural mortality, age 0	$M_{\text{age-0}}$	2.25 (0.45)
Proportion survival, overwinter mortality[a]	x	0.80 (0.16)[b]
Initial mortality	None	0.02 (0.06)[b]
Harvest	H	0.01 (0)
Delayed mortality, model 1	None	0.10 (0.05)[b]
Exploitation rate, model 1	e	0.13
Delayed mortality, model 2	None	0.30 (0.14)[b]
Exploitation rate, model 2	e	0.34
Size vulnerable to harvest	v_h	305 (30.50)
Size vulnerable to gear	v_g	200 (20.00)

[a]Parameter applied only to largemouth bass that were <100 mm.
[b]A beta distribution of variance was assumed because parameter estimate is a proportion.

to older age-classes was modified by the multiplier,

$$M_{\text{age-0}} = M \times x.$$

With this multiplier, survivorship for age-0 largemouth bass <100 mm was equal to approximately 8% (see Table 1). This value is within the range reported by Post et al. (1998), i.e., between 2.2% (in a cold year) to 26.4% (in a more benign year).

In the presence of a fishery, survivorship of an age-class to a subsequent age-class depends on M, as well as the proportion of largemouth bass that is vulnerable to harvest (u_h) and gear (u_g), with an exploitation rate (e) according to the expression:

$$1 \times [1 - (u_h \times u_g \times e)] \times M.$$

The vulnerability of each length-at-age-group (p_i) to harvest was modeled using an inverse function of the size limit (305 mm, SD = 30.5) for the Potomac River population of largemouth bass, i.e.,

$$1/\{1 + \exp[(305 - p_i)/30.5]\}.$$

Similarly, vulnerability of each length-at-age-group to fishing gear was modeled as an inverse function of the size of recruitment to the gear (200 mm, SD = 20.0):

$$1/\{1 + \exp[(200 - p_i)/20]\}.$$

A largemouth bass that is approximately 200 mm is considered stock length (Gablehouse 1984) and capable of being caught by anglers (J.W.L., personal observation). The SD estimates were arbitrarily defined as 10% of the size limit for both vulnerability to harvest and vulnerability to gear.

Sources of exploitation for largemouth bass on the Potomac River include initial mortality (mortality of bass vulnerable to gear and harvest during tournaments), harvest (mortality of bass vulnerable to gear and harvest, not during tournaments), and delayed mortality (or catch-and-release mortality of bass vulnerable to gear or harvest). The point estimates and estimate of variance for initial mortality (or the proportion of largemouth bass that died during a tournament) were measured from tournaments on the Potomac River between 2005 and 2011 (MDDNR 2012). Harvest by recreational anglers from the Potomac River was measured during creel studies (MDDNR 1995), but no variance estimate was provided or is known. Delayed mortality (>24 h) has been measured as the proportion of largemouth bass that died or was expected to die following sport fish tournaments during summer on the Potomac River (MDDNR 2012). Using data reviewed by Wilde (1998), a coefficient of variation (CV = 100 × SD/mean) in delayed mortality was estimated at 45%. Thus, variance in delayed mortality was estimated as 45% of the point estimate.

The impact of northern snakehead on age-0 largemouth bass was modeled to test our hypotheses that the snakehead would negatively affect the bass population, but that the effect of northern snakehead depended on e of largemouth bass. Two aspects of the largemouth bass population were studied: (1) the percent reduction in the abundance (S) of bass; and (2) percent reduction in the proportion of bass that were equal to or greater than 305 mm (i.e., legal harvest size in Maryland) in the population (i.e., proportional size distribution; PSD_{305}). The population model was used to predict the size of the unfished-state population (S_u), size of the fished-state population (S_f), and size of the fished-state population impacted by northern snakehead (S_{fN}). Percent reduction in S of largemouth bass was calculated as

$$[(S_u - S_f)/S_u] - [(S_u - S_{fN})/S_u].$$

The S_u was the sum of survivors among age-classes in the population model without assuming a fishery. The S_f was the sum of survivors among age-classes in the population model while assuming loss of individuals to the fishery. The S_{fN} was the sum of survivors among age-classes after modifying the proportion of age-0 largemouth bass entering age 1 (p_1) for the fished-state population by the level of predation by northern snakehead. The p_1 depended on the proportion of age-0 bass for the fished state population (p_0) that are vulnerable to predation (v) and are consumed (c):

$$p_1 = p_0 - (v \times c \times p_0),$$

where c was estimated from experimental tank experiments. Only the three sizegroups of age-0 largemouth bass were assumed to be vulnerable to predation by northern snakehead. Similar to these levels of S, the PSD_{305} was calculated for only the proportion that was 305 mm or larger (i.e., PSD_{305u}, PSD_{305f}, PSD_{305fN}). Percent reduction in PSD_{305} of largemouth bass was thus calculated as

$$[(PSD_{305u} - PSD_{305f})/PSD_{305u}] - [(PSD_{305u} - PSD_{305fN})/PSD_{305u}].$$

Percent reductions were averaged from iterative runs whereby parameters were recomputed each run using Monte Carlo simulations ($n = 1{,}000$). Unless it was a fixed parameter, variance for most parameters was assumed to be normal; variance in overwinter mortality and delayed mortality were assumed to have beta distributions to reflect infrequency in extreme mortality events. Monte Carlo averages for percent reductions were calculated across an incremental range of v (0–1.0, increment = 0.1) to determine how increases in the distribution of northern snakehead would affect the population. When v equaled 1.0, complete co-occurrence was assumed and age-0 largemouth bass were completely vulnerable to predation by northern snakehead.

To test the hypothesis that expansion of northern snakehead populations (i.e., increases in v) would adversely affect the abundance and PSD_{305} of largemouth bass, linear regression was used to determine if average percent reductions (dependent variables) varied positively with change in v (independent variable). To test the hypothesis that the effect of northern snakehead depended on e, for each level of v, percent reduction was calculated for two models with realistic levels of e (MDDNR 2012): 0.13 (model 1) and 0.34 (model 2) (Table 1). Delayed mortality estimates can vary depending on environmental conditions and angler disposition (Wilde 1998; Pope and Wilde 2004).

RESULTS AND DISCUSSION

Largemouth bass (27–720 mm) were spread throughout the study area (Figure 2), while northern snakehead (152–865 mm) were caught mainly in streams (Figure 3). Both juvenile bass and snakehead were distributed in upper tributaries. In addition to upstream areas of streams, northern snakehead also prefers shallow waters with soft substrate during autumn (Lapointe et al. 2010; J.W.L. and J.J.N., personal observation). These habitats are also highly suitable for largemouth bass. In general, highly suitable habitats for largemouth bass (Figure 2) were positively associated with the distribution of northern snakehead. Not all moderately or highly suitable habitats for the bass were occupied by snakehead. Of all 85 sites where juvenile largemouth bass occurred during autumn, northern snakehead only co-occurred at nine locations (10.6%). Both species co-occurred mainly in streams and particularly in subwatershed areas that comprised Mattawoman Creek (at 15% of 20 sites) and Chicamuxen Creek (at 33% of six sites) (Figure 3). In habitats of co-occurrence, predation can influence survivorship of juvenile largemouth bass and predation threat may negatively influence growth (Gilliam and Fraser 1987). If growth of age-0 largemouth bass is inhibited by northern snakehead, then odds of survivorship may be lower and recruitment negatively influenced. While not studied here, competition between adult northern snakehead and adult largemouth bass for limited resources may also negatively affect recruitment of bass if resources limit their gonad development or nest building behavior. While there is no evidence that resources are currently limiting reproduction, resource availability may change when watersheds are developed (Dauer et al. 2000; Uphoff et al. 2011). Further work is necessary to determine if competition between adults will limit growth or recruitment for largemouth bass and other species within Potomac River.

TABLE 2. Number of age-0 largemouth bass used in tank experiments and the percent that survived (in parentheses) after 7 d of vulnerability to predation by adult northern snakehead. For experiments, largemouth bass were grouped into three size-classes.

Size class (mm)	Trial 1	Trial 2	Trial 3	Trial 4
70–99	3 (67%)	4 (25%)	5 (60%)	5 (0%)
100–150	1 (100%)	2 (100%)	5 (0%)	
>150	1 (100%)	1 (100%)	1 (0%)	

In tank experiments, small (<100 mm TL) age-0 largemouth bass had lower survival than larger age-0 bass when they co-occurred with adult northern snakehead. On average, only 38% (0.38, SD = 0.31) of small bass survived per experiment (Table 2), resulting in a c (or proportion of age-0 bass that were consumed) of 0.62. In contrast, 67% (0.67, SD = 0.57) of the larger largemouth bass (>100 mm) survived per experiment, resulting in a c of 0.33. Similarly, Miranda and Hubbard (1994) used experimental ponds and reported lower survivorship of small age-0 largemouth bass (<126 mm) in the presence of predators. Tank experiments used here provide artificial conditions by design and may therefore have biased estimates of c. To address bias, sensitivity analyses were applied to c for largemouth bass. Varying c for small bass to some level within 20% of its value led to a change of 0.016% and 0.013% in the impact of the snakehead on bass abundance and PSD_{305}, respectively (when $v = 0.106$, $e = 0.34$). Similarly, by varying c for larger age-0 largemouth bass, there was a small change of 0.003% and 0.002% in the impact of snakehead on bass abundance and PSD_{305}, respectively. Thus, more refined estimates of c are encouraged, but should not greatly affect the interpretations from this model's outcomes.

The c values used here were obtained using feeding experiments that lacked refugia. Refugia (e.g., grasses) protect largemouth bass from predation and promote population growth (Bettoli et al. 1992; Miranda and Hubbard 1994; Hoyer and Canfield 1996). When refugia are available, survivorship of age-0 largemouth bass could increase to 80% (Miranda and Hubbard

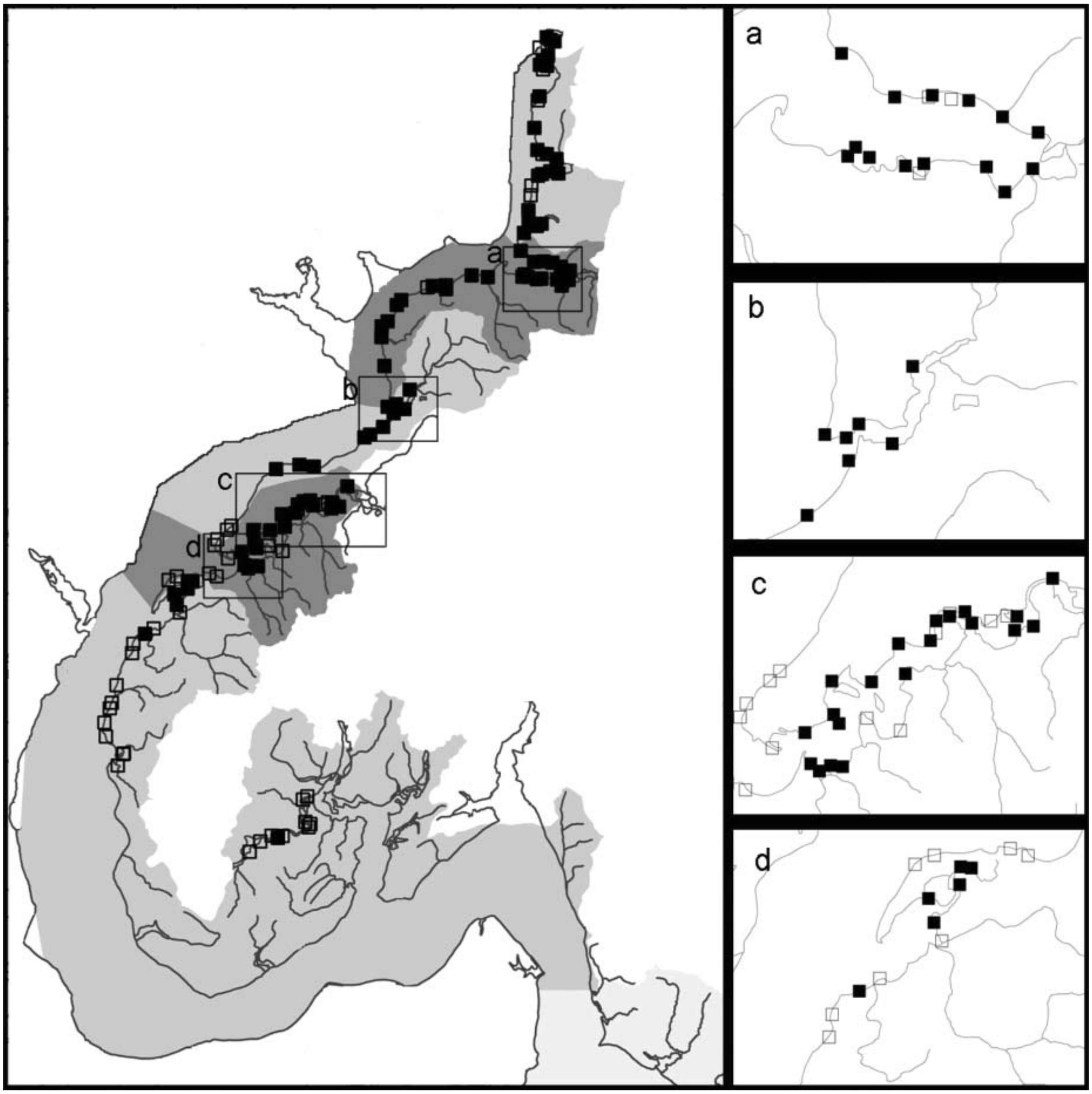

FIGURE 2. Potomac River (Chesapeake Bay) and the distribution of sampling sites (left panel) for the Maryland Department of Natural Resources Tidal Bass Survey (open squares = sampled site; solid squares = catches of juvenile largemouth bass, autumn 2008–2010). Shading of watershed area represents suitability for largemouth bass: dark grey = high suitability (>69%); medium gray = moderate suitability (65–69%); light grey = poor suitability (<65%). Right panels a–d represent expanded views of the selected areas in the left panel.

1994) from 10% that was estimated here from hatchery ponds lacking refugia. Even in the absence of refugia, adult northern snakehead did not consume all age-0 bass during the experimental tank experiments. In a natural setting, northern snakehead may preferentially select prey other than age-0 largemouth bass, thereby reducing their negative impact on the population and, ultimately, the largemouth bass fishery. More work is encouraged into prey preference of northern snakehead and influence of refugia on interactions between these two species.

At current levels of co-occurrence (or $v = 10.6\%$) and exploitation rate ($e = 0.13$), the population model predicted a 3.8% and 3.2% reduction in abundance and PSD_{305} of largemouth bass, respectively. Thus, the model indicated that the effect of northern snakehead on bass populations was minimal ($\leq$10% reduction in abundance and PSD_{305}; Figure 4) when the population of snakehead is controlled by maintaining v to less than 30%. Current surveys of largemouth bass have not indicated declines in abundance or PSD_{305} since the introduction of northern snakehead (MDDNR 2012), which would be expected at current levels of v. Future expansion of northern snakehead in the Potomac River will probably have negative effects on the largemouth bass fishery. As v increased to 100%, there was up

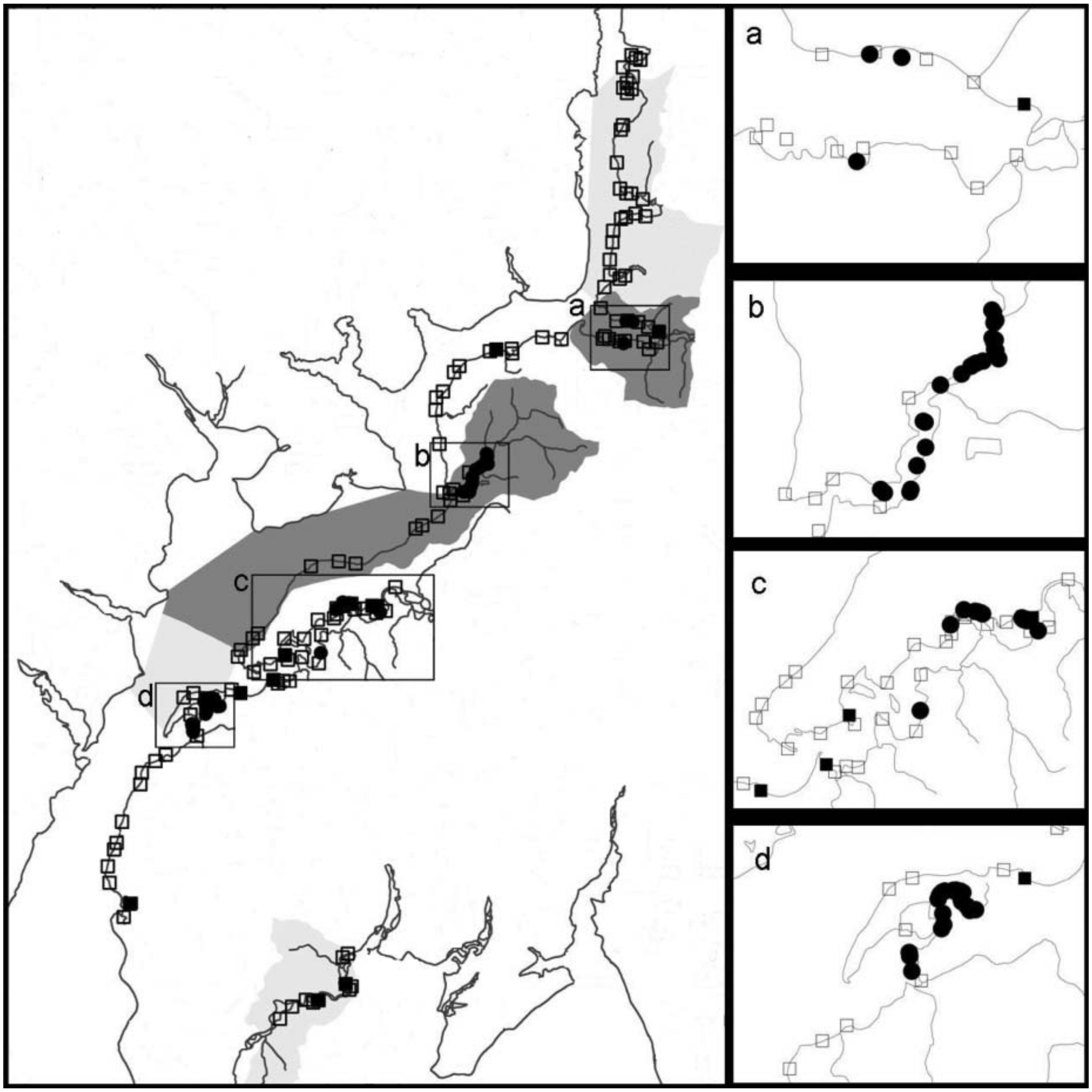

FIGURE 3. Potomac River (Chesapeake Bay) and distribution of sampling sites (left figure) for the Maryland Department of Natural Resources Tidal Bass Survey (open squares = sampled site without northern snakehead; solid squares = catch of northern snakehead [autumn 2008–2010]) and for the U.S. Fish and Wildlife Service (solid circles = catch of northern snakehead, autumn 2009–2010). Shading of watershed areas represents areas where co-occurrence between northern snakehead and juvenile largemouth bass was high (dark grey, >10% of sites with co-occurrence), moderate (medium grey, 1–10%), and poor (light grey, <1%). Right panels a–d represent expanded views of the selected areas in the left panel.

to a 35.5% (0.355, SD = 0.13) reduction in largemouth bass abundance and 30% (0.030, SD = 0.21) reduction in PSD_{305} (Figure 4). Increases in v may also occur if there is a loss of refugia or submerged aquatic vegetation (SAV). Changes in the distribution of SAV periodically occur within the Potomac River (Orth and Moore 1983) and may lead to greater interactions between the snakehead and bass. The time required for expansion of northern snakehead populations or until such changes in the environment is not known; therefore, it is not currently possible to state that northern snakehead pose no threat to the Potomac River ecosystem. Continued vigiliance in controlling the spread and biomass of this species is encouraged.

The influence of v was particularly noticeable when e of largemouth bass was low. When e was 0.13, the level of northern snakehead impact increased more sharply with v than when e was 0.34 (Figure 4), as hypothesized. Exploitation rates for largemouth bass influenced the impact of northern snakehead on the bass population. When e was approximately 0.34 and co-occurrence increased beyond 40%, then the impact of the snakehead on largemouth bass abundance and especially bass

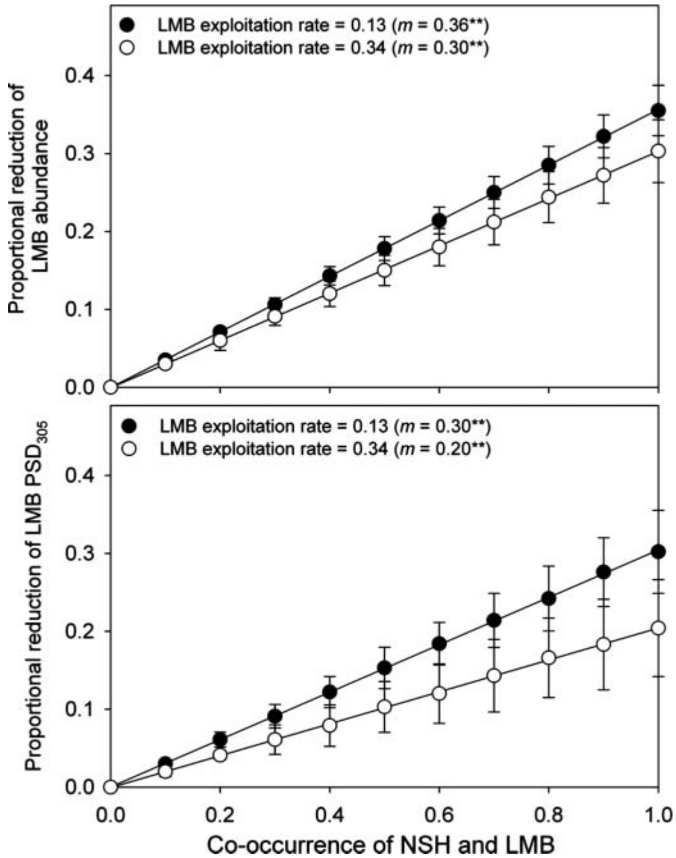

FIGURE 4. Proportional reductions in largemouth bass (LMB) abundance and proportion of fish greater than 305 mm TL (proportional size distribution, PSD_{305}) as co-occurrence between bass and northern snakehead (NSH) increases. The slopes (*m*) for values calculated at two levels of exploitation rate are provided with asterisks that illustrate significance ($^{**}P < 0.01$) from an analysis of covariance (ANCOVA). Bars are ±SE of the mean.

PSD_{305} significantly lessened (Figure 2; analysis of covariance [ANCOVA], abundance $v \times e$: $F_{1,18} = 3{,}930$, $P < 0.0001$; PSD_{305} $v \times e$: $F_{1,18} = 4{,}548$, $P < 0.0001$). In that case, angler exploitation of largemouth bass diminished the impact of northern snakehead on the population. As adult bass die from catch-and-release mortality, fewer are available in the population and less variance in abundance or PSD_{305} can be attributed to the effect of northern snakehead. When *e* equaled 0.34, there was also greater variation in estimates of the snakehead impact on abundance and PSD_{305} (Figure 4). Thus, higher exploitation rates led to greater uncertainty in the predicted impact of northern snakehead on largemouth bass abundance and PSD_{305}.

Exploitation rates can vary seasonally, with greater delayed mortality occurring during warm water temperatures during summer (Wilde 1998; Ostrand et al. 2011) and nest failures during spring (Gwinn and Allen 2010). Estimates of delayed mortality used here are observed extremes for the Potomac River and are similar to those reported elsewhere (Ostrand et al. 2011). In some cases, exploitation may also arguably include a loss of juveniles during spring because of nest failures caused by high levels of catch-and-release angling coupled with adult displacement (Gwinn and Allen 2010). Current data indicate that angling effort during spring is not sufficient to negatively affect populations of largemouth bass (J.W.L., unpublished data). If exploitation rates increase in the future, then the predicted impact due to the expansion of northern snakehead should likewise decrease. We do not expect exploitation rates for largemouth bass to increase on the Potomac River, at least in the near future, because anglers have generally adopted no-harvest ethics (Allen et al. 2008; Wilde and Pope 2008). Angling effort from tournaments has also not significantly increased for the past decade (MDDNR 2012).

In addition to interactions with northern snakehead and anglers, the number of largemouth bass that survive to age 1 can depend on size-selective overwinter mortality (Ludsin and DeVries 1997; Post et al. 1998; but see Peer et al. 2006). This aspect of recruitment was accounted for in the current population model, but accurate estimates of overwinter mortality are not known. The Chesapeake Bay and Potomac River experience cold winters (e.g., December–March 2010, <10°C; NOAA National Data Buoy Center, station TPLM2) that are potentially capable of limiting recruitment of largemouth bass. Cold winters (<10°C water temperature) are expected to reduce survivorship of small age-0 largemouth bass more than large age-0 bass (Ludsin and DeVries 1997; Post et al. 1998). Both overwinter mortality and predation by northern snakehead may lower the number of bass recruiting into the population.

The current research indicates that while the impact may be relatively minimal, maintaining co-occurrence to 30% or less of suitable habitats (possibly greater with protective refugia) would help protect the largemouth bass fishery in the Potomac River. At greater levels of co-occurrence, the negative impacts of northern snakehead on the bass population are lessened when exploitation rates for largemouth bass are high. Mechanisms that limit the spread of northern snakehead are not known. Northern snakehead colonizes new habitat commonly after high rainfall events and during spring (J.J.N., unpublished data). High rainfall events during spring may facilitate the spread of invasive species (Rahel and Olden 2008; J.J.N., unpublished data). Watershed management strategies (e.g., dam removal) that increase confluence among streams may also facilitate expansion of the species. Once a habitat is colonized, persistence in naïve habitats (i.e., successful colonization) depends on whether favorable environmental conditions exist, which should be indicated by the native range of northern snakehead (Wiens and Graham 2005). If northern snakehead favor similar habitats as largemouth bass, as suggested by this study, then many suitable habitats have yet to be successfully colonized by northern snakehead in the Potomac River. The persistence of invasive species in naïve habitats is often plausible because aquatic communities are rarely saturated with species (Sax et al. 2007). Biological control methods for invasive species, such as introducing natural predators have been applied in a few cases, but with often unintended, negative consequences (Messing and Wright 2006). There are no known natural predators for large northern snakehead in North America, aside from humans and possibly some birds of prey. Thus, control measures aimed at human removal of northern snakehead from all habitats, particularly newly colonized ones, is strongly encouraged for continued protection of aquatic ecosystems.

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